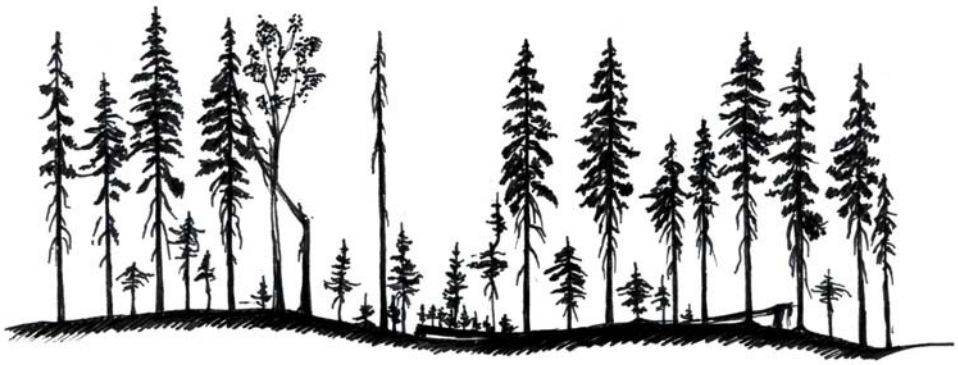
250 Years of Disturbance Dynamics in a Pristine Old-growth *Picea abies* Forest in Arkhangelsk Region, North-Western Russia: a Dendrochronological Reconstruction



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Swedish University of Agricultural Sciences
Master Thesis no. 163
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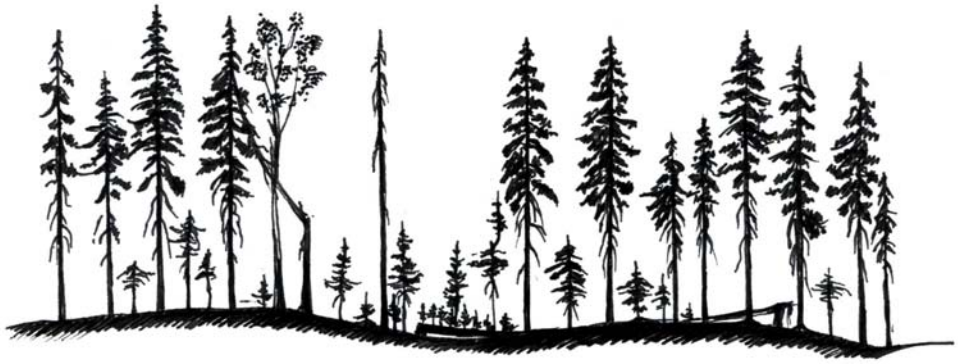

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Abstract

To describe the historical patterns of natural disturbance regimes in European boreal forests we conducted a dendroecological study in a primeval old-growth spruce dominated stands and reconstructed the long-term dynamics of canopy disturbances. We treated the radial growth releases of individual sub-canopy trees as the major indicator of sudden openings in the forest canopy. Growth releases were detected by using the formal approach only (strict criteria were applied). The reconstruction of past canopy disturbances was done by GIS-based analysis of spatial information on released trees over the study period.

The study area was located in the transitional vegetation zone of the middle and northern taiga, on the watershed of Northern Dvina and Pinega rivers, North-Western Russia.

Spatial and temporal characteristics of canopy disturbances were studied within the area of 1.8 ha along the two transects, 20x450 m^2 each. All trees with DBH > 6 cm (dead and alive) and coarse woody debris (DBH > 18 cm) within transects were mapped and described (n = 2126) and all living and recently dead trees were sampled with an increment corer (n = 1678) at the height 40 cm above the root collar.

Stands were composed of *Picea abies* and *Betula pendula*, mean standing volume was 211 m^3/ha.

Spruce was of multiple ages with pronounced regular peaks (cohorts) in trees age distribution. At least four such cohorts were distinguished and represented peaks in spruce regeneration.

No evidence of stand replacing events was found over the 250(300)-year period that the study covered. The dynamics was likely driven by small and middle-size canopy disturbances, occurring at varying frequencies. A detailed spatial disturbances reconstruction reflecting the last 170 (160) years revealed a disturbance rate of about 4% yearly mortality. Periodic increases in disturbance rate however played a major role in forest regeneration. Four such peaks were timed to decades 1850, 1890, 1930 (1920 – for transect 1) and 1980. Disturbance rates at peaking decades were about 60% and never exceeded 75% of the canopy area.

Surprisingly little difference in disturbance rates was found among forest types with different soil moisture. Though forests with higher soil moisture had slightly lower disturbance intensity and less pronounced regular peaks in disturbance rate over considered time span.

Keywords: Forest history, disturbance dynamics, disturbance, canopy gap, disturbance rate, old-growth forest, Norway spruce, European spruce bark beetle, dendrochronology,.

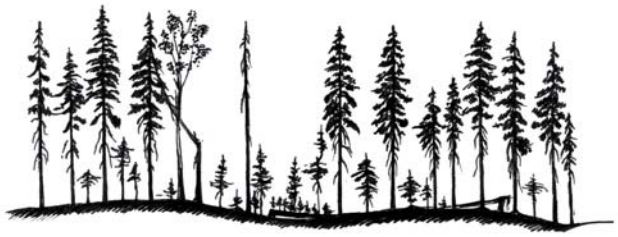
Introduction

Canopy disturbances have long been recognized as a fundament factor in natural forest dynamics, predetermining major stands characteristics (Kuuluvainen, 2002; Gromtsev, 2002). Scale and frequency of the regular openings in the forest canopy strongly affect species variability, forest structures and functions (Fraver and White, 2005a). Differences in prevailing patterns of natural disturbances cause multiple pathways of forest dynamics (Shorohova et al., 2009), known as the forest disturbance regimes. Better understanding of these pathways is becoming increasingly important in order to formulate a scientific base for designing nature-based forest management strategies, conservation of species and habitats diversity (Nilsson et al., 2001; Angelstam, 1998), and restoration of significantly altered or degraded forest ecosystems (Kuuluvainen, 2002).

Factors of different nature, from the different perspectives contribute to the disturbance regime. They strongly influence rotation of generations and abundance of species with different ecological requirements. The most powerful ecological factor shaping forest structures and dynamics in the boreal vegetation zone is fire (Gromtsev, 2002; Ryan, 2002; Niklasson and Granström, 2000). It provides the major differences among forests types and species variability.

The long-term spruce dominance, for which the favorable conditions were found on the flat watersheds of European taiga, points out that fire in some areas play a limited role. Insects, wind (Shorohova et al., 2008), fungus attack (Lannenpaa et al., 2008) and summer droughts (Aakala and Kuuluvainen, 2010) are here the main trees mortality argents. Fire return intervals here exceeded 300 years and potentially even 1000 years (Wallenius, 2002; Wallenius et al., 2005). Lack of stand replacing events provided limited opportunities for regeneration of pioneer, light demanding, tree species (Drobyshev 1999). Such old-growth spruce dominated forests are characterized by low fertility, rather high soil moisture and poor compositional variability. Canopy composition is often limited to two groups of species with the opposite light requirements. (Fig.1). Canopy recruitment commonly occurs in the gaps of a small and middle size, initiated by the death of one or several canopy trees (Fig.1).

Old-growth spruce stands of North-Western Russia, however reveal periodical deviations from the normal small-gap disturbance regime (peaks in disturbance rates), which seem to become a pattern (*field observation*). These deviations are responsible and vital for recruitment of light demanding species into the forest canopy and increase of biodiversity (Fig.1).



a)

b)

c)

d)

Figure 1 (a, b, c, d). Scheme of old-growth spruce dominated stands dynamics, driven by small and middle size canopy gaps. (a) The main canopy in the old growth spruce dominated forest is never 100% closed. Forest is characterized by the presence of trees of various canopy positions, deadwood at different decay stages, dead standing trees and snags. Furthermore the share of light demanding species (birch) is strongly limited by competition with shade tolerant spruce. (b) The dynamics is commonly driven by the death of single trees or groups of trees in the forest canopy. (c, b) Formation of larger canopy gaps is vital for light demanding species regeneration.

Forest dynamics involve a very large range of spatial and temporal disturbance scales. For reliable and practically applicable results studies must be carried in large unfragmented and minimally altered forest areas, which provide the sufficient source of information for long term disturbance history reconstruction. Studying of natural dynamics at a "priory time periods or spatial extent" may disserve to a forest management practices (Landres P.B. et al., 1999). In this context the scarcity of boreal forests, which have not yet experienced the influence of human activity is posing challenges for scientific research. Remnant old-growth taiga ecosystems very rarely occur at a large extent (Potapov et al., 2008; Yaroshenko A. et al., 2002; Aksenov D. et al., 2002). It makes studying of natural disturbance dynamics difficult.

Most of previous studies have focused on old-growth forests at rather high elevations, steep slopes, or were spatially limited to small areas within the extensively fragmented boreal forest. At appropriate scale the disturbance dynamics were studied in Northern America (Fraver et al., 2009; Rowland and White, 2010) and in the remaining small inaccessible forests of Fennocandia (Fraver et al., 2008; Linder, 1998; Aakala et al., 2009).

In Russia relatively large unmanaged taiga ecosystems can still be found in remote areas of the Northern European provinces. We located our study to the largest remained old-growth forest area in the Russian boreal zone, located on the flat watershed between Northern Dvina and Pinega rivers.

The study aimed to reveal the major trends of natural disturbance dynamics in late-successional dark-coniferous taiga, long time dominated by Norway spruce (*Picea abies*), and to explain the long term interplay between spatial and temporal characteristics of canopy disturbances.

To reconstruct past disturbance events we examined radial growth patterns of sub-canopy trees, using dendroecological techniques. Dendroecology is recognized as one of the most effective methods to reconstruct past disturbance events with both high spatial and temporal resolution (Fraver et al., 2009).

Disturbance rates were reconstructed for every decade over the 250(270)-year period by delineation of trees, which were released from sub-canopy positions.

Four main questions were addressed:

- What is the age structure of old-growth spruce stands?

- What are the historical disturbance rates and its variability?

- What were the temporal and spatial patterns of natural disturbances over the last several centuries?

- Do the soil conditions affect the disturbance rates and disturbance dynamics?

Results of the study demonstrate the use of well-established combined methods (GIS-aided analysis and dendrochronological techniques) and should be viewed as an initial attempt of data interpretation. We plan to revisit it while preparing the material for publication in an international journal.

Material and methods

Study area

The study was conducted in an old-growth pristine spruce-dominated forest of Archangelsk province, North-Western Russia (N 63º 15´, E 43º 49´, Fig. 2, 3).

The regional climate is strongly influenced by vicinity of the White Sea. Mean annual temperature is 0.9 ºC, mean annual precipitation 600 mm. The coldest month is January with mean temperature -14.1ºC, the warmest month is July with a mean of 16.1ºC. Prevalent wind direction is west-east with mean annual speed 3.8 m/s. Once in 5 years the wind speed can rise up to 17 m/s (WWF, 2006). Major part of the watershed is flat. Elevation does not exceed 267 m above the sea level (Zagidullina, 2009); within studied area elevation ranged between 180-210 m. The dominant soils are poorly drained loams and sandy loams of low fertility.

In this area old-growth forests cover central part of the watershed between Northern Dvina and Pinega rivers (Fig.2), which pertains to the transitional vegetation zone between middle and northern taiga. The landscape is predominantly occupied by spruce stands (82.3%) on wet sites, with pine and birch stands being present on 10.1% and 7.6% of the area, respectively (WWF, 2006). In total about 94% of the study area is forested. The dominant series of forest types are polytrichoso-myrtillosum and myrtilloso-sphagnosum with Carex globularis and Equisetum sylvaticum (Zagidullina, 2009).

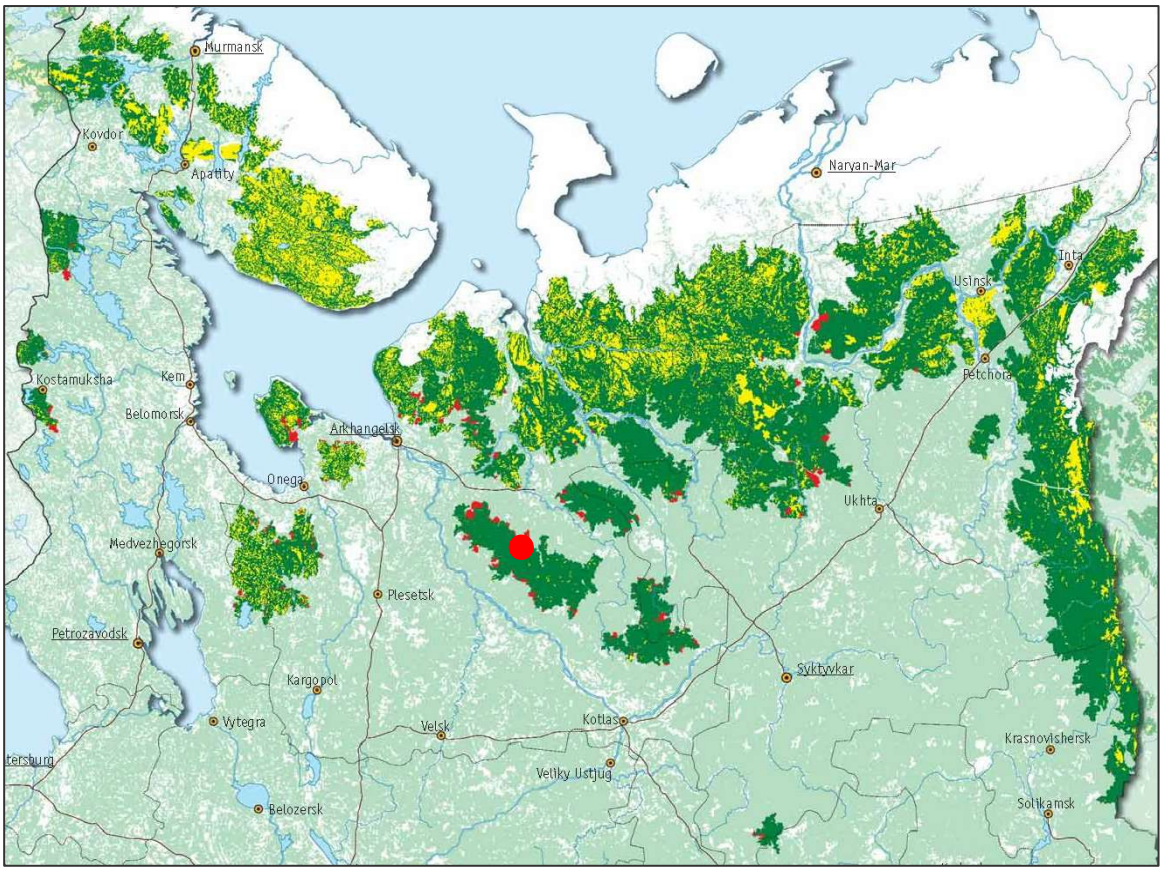


Figure 2 Fragment of the map “Intact Forest Landscapes of Northern European Russia (Greenpeace Russia, 2004). Study area is marked with red dot.

In 2002 the studied forest area was designated as one of the last Russian’s Intact Forest Landscapes (IFL) (Fig.1), i.e. a forest without significant signs of the past human activity and large enough to maintain "all native biodiversity, including viable wide-ranging species populations" (Aksenov D. et al., 2002). Total area of the IFL in 2006 was 1 043 672 ha (Greenpeace Russia, unpublished data). The forested area diminishes every year due to intensive logging activity, the most significant changes being over the most recent decades. Still the landscape embodies one of the biggest HCVF2 (second category of High Conservation Value Forest, according to FSC classification (FSC, 1996)) in the middle taiga zone of the European part of Russia (Yaroshenko A. et al., 2002).

History of forest development

The watershed between Northern Dvina and Pinega rivers was dominated by spruce forests at least over the last 500 years (Zagidullina, 2009), possibly much longer - no specific studies of pollen were made in the area.

The remote location and lack of roads have limited human influence and the forest ecosystems display natural structures and dynamics. Selective cuttings might have taken place locally during 19-20 centuries (Kuznetsov, 1912), when only a limited number of the best quality trees were removed from the stands.

Stand replacing disturbances were not apparently the dominating factor of natural dynamics of the studied forest. High soil moisture and of prevailing loams underlies the low frequency of natural fires - the important factor defining long-term disturbance regime in the boreal forests. Fire return interval here was longer than the time span covered by dendrochronological study, and likely exceeds 300 years (Wallenius, 2002; Wallenius et al., 2005). Stand replacement might have been occasionally caused by wind-through, but apparently, in majority of spruce dominated stands on the watershed the succession was driven by small and middle scale gap-dynamics (Yaroshenko A. et al., 2002).

Along with continuous mortality of single canopy trees, two major pulses of disturbance intensity were recorded in this area over the last century. At the end of 18th and beginning of the 19th hundreds the insect outbreak resulted in nearly 50% spruce mortality (Kuznetsov, 1912). Trees were dying in groups shaping horizontally clustered forest canopy structure. The most recent and very similar disturbance pulse is known from 2001. Prior to disturbance weakening of trees was likely initiated by repeated droughts in the summers of 1997-1998 and snow-breakage in the winter of 2001 (Ogibin and Demidova N.A., 2010). However the ultimate mortality factor was a massive outbreak of *Ips typographus* (European spruce bark beetle).

Site selection

Field data was collected in the central part of an old-growth spruce forest on Dvina-Pinega watershed. The area represented dark coniferous stands, typical for flat wet areas in European taiga zone. Selection of the area was based on (1) analysis of satellite imagery and (2) direct assessment of forest stands in the field.

For satellite imagery analysis we used false color images from Landsat 5 TM from 2006 (spatial resolution 28.5 m, band combination 5-4-3). The following criteria were used for stands selection: predominantly dark-green color on the image of selected area, location of the stands at least 120 m from old-established roads and clear cuts (older than 10 years); the latter criterion was used to avoid edge-effects, resulting in increased rate of canopy disturbance rates on the border between pristine old-growth forest and large clear cut areas (Khakimulina, 2008).

During outdoor assessment the stands were selected as appropriate for sampling, if no evidence of past human activity was observed. Such stands were lacking the signs of past human activity - decaying/decayed cut-stamps larger than 18 cm in diameter.

Field sampling design

Field sampling was designed to maximize the analyzed area size to consider both small gap dynamics (size of the single patch $<10^2$ m^2) and relatively large disturbances (~ $10^{3\text{-}4}$ m^2).

Sampling was done within two transects (Fig. 3), 450×20 m^2 each, with total coverage of 1.8 ha. Transects were designed as a spatially continuous array of 20×20 m^2 plots (except for the ending plots, which dimensions were 20×10 m^2).

To decrease spatial autocorrelation in canopy disturbances, minimal distance between transects was chosen to exceed their length (~500 m vs. 450 m).

Both transects were predominantly South-North oriented, crosswise to the dominating wind direction. Such design helped to avoid potential bias in estimation of canopy disturbance rates due to probability of wind caused elongated gaps and transect axes coincidence.

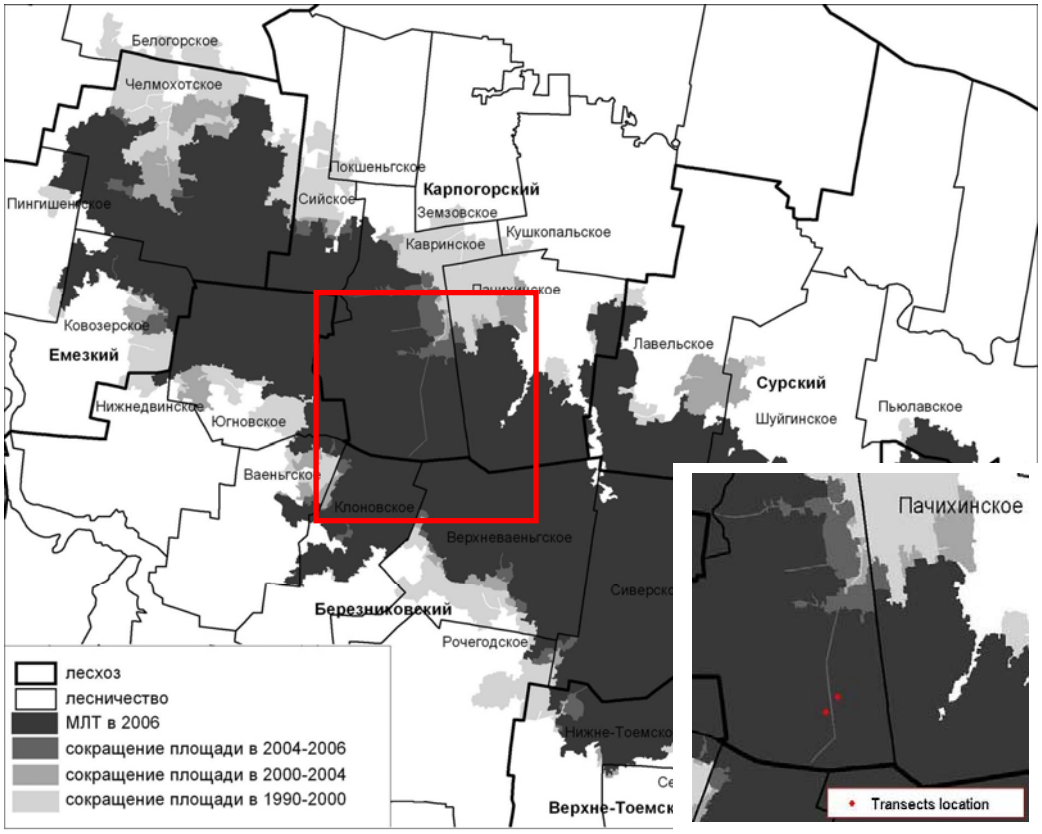


Рис 1. Сокращение площади лесного покрова в Двинско-Пинежском массиве в 1990-2006 г.г.

Figure 3 Transect location within Intact Forest Landscape (fragment of map by Greenpeace of Russia, 2006).

Both transects were placed randomly within the dominant topographical elements, i.e. upper parts of the flat slopes gently rolling towards small forest streams. Forest vegetation types here varied among Piceetum *Myrtillosum*, *Polytrichoso-myrtillosum* and *Myrtilloso-sphagnosum* (Fedorchuk et al., 2002), and represented heterogeneity and locality of soil characteristics. In the forest the borders of transects were temporally line-marked.

Within transects all living trees (dbh ≥ 6 cm) and coarse woody debris (DBH > 18 cm) were mapped and described. We sampled all living trees and deadwood at 1 and 2 decay stages (Shorohova and Shorohov, 2001)Trees were cored by increment corer at the height of 40 cm above root collar, and in a direction perpendicular to eventual leaning of the tree - side of the stem judged to be free of compression wood.

For each transect we recorded: (1) axis direction, (2) geographic coordinates of the beginning and the end points (using GPS unit Garmin-12), (3) position of recent (formed during the last decade) and old canopy gaps and (4) mean canopy height (measured by altimeter), calculated separately for spruce and birch as average of nine trees, representing three the most frequently occurred diameter classes. Trees were

selected at the beginning and the end of each transect. (5) mean crown size for each tree species.

For each sample plot (20 x 20 m) we recorded: (1) geographic coordinates of plot's mid-point, (2) absolute coordinates of the plot's mid-point (distance from the beginning point of transect, m), (3) local topography (slope exposition and steepness), (4) floor vegetation (dominant species only and their coverage, in %).

For each tree/deadwood were recorded: (1) absolute coordinates (Y = distance along central transect axis, X = shortest distances (beeline) from the central axis (measured with 10 m tape and accurate within 0.1 m), (2) species identity, (3) life status (alive or dead), (4) deadwood characteristic (standing dead tree, snag, uprooted tree or stamp), (5) relative canopy position of living trees (D, C, I, O - dominant, co-dominant, intermediate, overtopped), (6) diameter at breast height (DBH), (7) decay class (for deadwood only).

Field data collection was conducted in June-July 2009.

Laboratory procedures

Samples were analyzed at DELA, Dendrochronological laboratory at the Southern Swedish Forest Research Center, SLU, Alnarp.

All collected samples were mounted on the woody sticks, sanded with up to 400 grit sanding paper and scanned with resolution 3200 or 2400 ppi, depending on the sample length and ring visibility. Tree rings were cross-dated using pointer years (Stokes and Smiley, 1968) and then measured in CooRecorder 7.1 program. For samples with missing pith the number of lost rings was estimated using pith locator. We followed this procedure for spruce cores with estimated number of missing pith rings not exceeding 25. The age of trees was calculated as a sum of rings number on sample and number of missing rings, suggested by pith locator.

Although we measured both the most dominant species (spruce and birch), uncertain crossdating of birch samples and excessive rot in made it difficult to use birch chronologies for further analyses. Thus birch samples were only used to estimate age of the trees in cases when pith was present on the sample.

Data processing

Defining general stand characteristics

Stand volume was calculated according to the official Russian table of tree volumes, specified for Arkchangelsk region.

To avoid the effect of the most recent large-scale disturbance event in the studied area, stand characteristics were back-calculated to the year of the last European bark beetle outbreak initiation (approximately dated to the year 2000). For this all deadwood at 1 and 2 decay stages were assumed to be living trees before the outbreak (Khakimulina, *personal observation*).

Preface to the method of forest history reconstruction

We analyzed growth patterns of all sampled spruce trees. Abrupt increases of trees radial growth (releases) were interpreted as trees growth response to the local canopy opening. Reconstruction of past canopy disturbances was based on identification of such releases shown by individual sub-canopy trees and GIS-added analysis, which helped deduce size and position of past canopy gaps from spatial information on all released and non-released trees in the stand.

Generally, three data sources were used to acquire the information about past disturbance dynamics. First, we analyzed *age structures* for two dominant canopy tree species (spruce and birch), to evaluate presence of separate age cohorts, indicative of past disturbance events. Second, we tracked the percentage of detected radial *growth releases*, shown by spruce trees, and its change over time. At the last step, linking trees spatial positions with their growing histories, we reconstructed spatial characteristics (or intensity) of natural disturbances at different decades by delineating canopy gaps.

The historical reconstruction included several methodological challenges. This includes to defined criteria for release detection, i.e. how abrupt and sustained should be release and to what degree the radial growth should change to indicate canopy disturbance? How to deal with phenomenon of compression wood and climate signals in growth chronology. How can we assure correct extrapolation of spatial information on canopy gaps into the past?

These problems were addressed by establishing a series of specific criteria.

Diameter threshold for release detection

To minimize the risk of considering climate-induced growth dynamics as growth response to canopy disturbances, we used only the sub-canopy trees for release analysis. To consider exclusively sub-canopy trees over the whole analyzed period, we retrospectively estimated sizes of all trees using available tree-ring chronologies. We used a diameter-based threshold to classify trees into two groups: canopy trees (not used in the analyses) and sub-canopy trees (used in the analyses).

Diameter threshold was estimated through analysis of distribution of trees canopy positions over diameter classes (Fig.4), and for overtopped and intermediate trees (sub-canopy categories) set as 18 cm. Based on this, trees less than 18 cm were assumed to be sub-canopy trees. Thus, only releases at diameter less than 18 cm were taken into account while reconstructing disturbance dynamics.

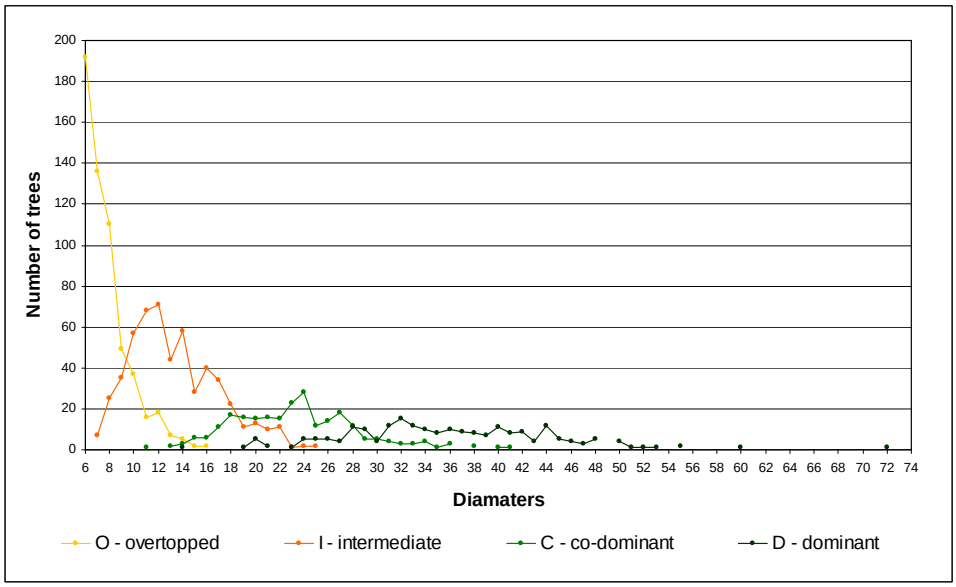


Figure 4 Diameters distribution of spruce in relation to four different canopy positions (D, C, I, O)

Release detection (method and criteria)

Radial growth releases were detected by using the formal approach only (strict criteria were settled). We based release identification on a simple percent increase method, using formula of (Nowacki and Abrams, 1997), which implements smoothing original growth chronologies by running averaging:

$$\%GC = (M_2 - M_1)/ M_1 \times 100,$$

where %GC is percentage growth change for a single year, M_1 and M_2 – the average radial growth over preceding 5 years and subsequent 5 years, respectively.

The five-year running mean window excluded release detection in the last years of growth chronologies and the latest reported year was set to 2004.

A minimum of 10 years between reported releases were fixed as criteria for release sustention. Calculations were done in *JOLTS*. For further analysis we used only the major releases, where percent-growth change exceeded a minimum threshold 100%.

Spatial analysis on release data (methods and criteria)

Percentage of released trees can be interpreted as a disturbance rates (Fraver and White, 2005b). The random allocation of trees in the forest, however, may cause an uncertain error in estimations. It is especially important in the studied forest, since analyzed sub-canopy trees were spatially clustered. In this study, we verified estimated area-under-gap value by comparing it with a direct empirical estimate.

Spatial patterns of canopy disturbances were reconstructed and analyzed at 10-year intervals (decades) in *ArcGIS 9.3 (ESRI 2009)*.

The approach to gap delineation was based on back-extrapolation in time of the spatial data on released trees. For this we calibrated *ArcGIS* criteria for depicting spatial release data (dated to the period 2001-2004 - the latest period of the radial growth chronology with extracted releases, started after the insect outbreak ignition) to the actual gap area. To avoid overestimation of disturbance rate, the actual gap areas for calibration were back-reconstructed to the last year of the same period - 2004.

To make it work in ArcGIS, the analysis process was sub-divided into three steps:

1) *Delineation of actual gaps (methods and criteria)*;

2) *Calibration of criteria for spatial analysis*, maximally matching the actual gaps (Kriging, calibration);

3) Back-extrapolation of disturbance rate.

1) Delineation of the actual gaps

Present gaps were delineated by drawing the canopy projection of the mapped trees: adding 3 m radius buffer zones around dominant and co-dominant canopy trees. For spruce this radius was purposely assumed as the actual mean crown size multiplied by 2, to cover interspaces between neighboring canopy trees.

Canopy projection, was based on the following categories of trees: all living trees and deadwood at 1th decay stage as trees, which died during the last insect outbreak, and was not yet reflected in the radial growth patterns of adjacent sub-canopy trees.

Transect 1

Transect 2

Figure 5. Distribution of trees with projected canopy and canopy gaps along the two transects. Light green is canopy projection, black - actual gap areas.

2) Calibration of criteria for spatial analysis

We used *Ordinary Kriging* as a method for spatial analysis on release data in *Geostatistical Analyst* in *ArcGIS.* To run the analysis, all trees were set to one of two values: 1 – for released spruce, 0 – for all present non-released trees. Trees were assumed to be present during a given decade if sample projected pith pointed to any year within the decade in question.

Calibration of criteria was based on both: qualitative (visual) and quantitative collation of (1) explicit gaps - delineated *actual canopy projection,* and (2) various *Kriging* results from analysis with different criteria applied.

Quantitative collation of results was done for 20x40 m2 segments of each transect. The only exception was made for dimensions of ending plots of transect, due to non-integer plot number.

Following criteria for Kriging were accepted:

Type – *Ordinary Kriging*;

Output type – *Probability*;

Primary Threshold – *0.5*;

Searching neighborhood: *type – standard, neighbors to include – 4, include at least – 2, full sector type*;

Variogram – *semivariogram, number of lags – 12*;

Model type – *circular*.

3) *Back-extrapolation of disturbance rate*

Kriging-based extrapolation of disturbance rates was being proceeded before the number trees within each transect dropped below 150. Thus the time span considered was limited to 170 years for 1th transect and 160 for 2th transect.

Defining influence of forest typology on disturbance history

Forest types varied through the transect interior.

We examined the correlation between forest types and historical patterns of disturbance dynamics according to degree of drainage (soil moisture). For each 20x20 m2 plot was defined one of three drainage degree (Chertov, 1981) according to percentage of *Sphagnum* in the moss layer:

<5% of *sphagnum* – normal drainage (low soil moisture);

from 5 to 40% of *sphagnum* – insufficient drainage (medium soil moisture);

>40% of sphagnum – poor drainage (high soil moisture).

Results

We mapped in the field and described **2126** trees and CWD (cause woody debris); **1678 (78.9%)** of them were sampled. Deadwood was represented by 243 trees or 14.5% of the taken samples. Cored trees were of three species: Norway spruce – *Picea abies* (n = 1525, or 90.9 % of the total sample number), silver birch – *Betula pendula* (n=234, 14.0%), and rowan – *Sorbus aucuparia* (n = 19, 1.1%).

Stand characteristics

The main canopy of the strands was composed of two tree species: *Picea abies* and *Betula pendula*. Spruce was an explicit dominant in the studied stands with 73% of the mean standing volume, 75% of the basal area and 93.6% of tree number. Average for two transects stand volume was 211 m3, absolute basal area – 21.5 m2 (Table 1).

Stand characteristics differed between two transects. Second transect had a higher tree density - 914 vs. 647 trees/ha (Table 1), mainly, due to the higher number of under-canopy trees. Absolute basal area was 20 and 23 m2 for the 1th and 2th transects respectively. Stand volume ranged between 198 and 224 m3 (Table 1).

The most recent European spruce bark beetle *(Ips typographus)* outbreak significantly affected characteristics of the spruce dominated stands (Table 1). It caused mortality of considerable share of spruce in the main canopy (113 m3/ha (42.3%)) (Fig. 6), as a hosting species for bark beetles. Average stand mortality for all species was estimated as 130 m3/ha, which is about 38.1% of the expected pre-outbreak stand volume (Table 1).

Table 1. Stands characteristics, calculated for the year of field data collection (2009), and back-calculated for the year of the recent insect outbreak initiation (2001).

Stand characteristics		***Stand characteristics at the year of data collection(2009)***			***Prior to outbreak stand characteristics, back-calculated to the years 2001***			***Mortality and reduction of characteristics since initiation of the insect outbreak in 2001, absolute value (percentage)***		
		Transect 1	*Transect 2*	***Both transects***	*Transect 1*	*Transect 2*	***Both transects***	*Transect 1*	*Transect 2*	***Both transects***
Number of trees, N/ha	*Spruce*	583	862	**723**	762	1024	**893**	179 (23,5)	162 (15,8)	**170 (19,0)**
	Birch	64	52	**58**	94	74	**84**	30 (31,9)	22 (29,7)	**26(31,0)**
	Total	**647**	**914**	**781**	**856**	**1098**	**977**	**209 (24,4)**	**184 (16,8)**	**196 (20,1)**
Absolute basal area, m2/ha	*Spruce*	14	18	**16**	26	28	**27**	12 (46,2)	10 (35,7)	**11 (40,7)**
	Birch	6	5	**5,5**	7	7	**7**	1 (14,3)	2 (28,6)	**1,5 (21,4)**
	Total	**20**	**23**	**21,5**	**33**	**35**	**34**	**13 (39,4)**	**12 (34,3)**	**12,5 (36,8)**
Standing volume, m^3/ha	*Spruce*	139	169	**154**	261	274	**267**	122 (46,7)	105 (38,2)	**113 (42,3)**
	Birch	59	55	**57**	73	73	**74**	14 (19,2)	18 (24,7)	**17 (23,0)**
	Total	**198**	**224**	**211**	**334**	**347**	**341**	**136 (40,7)**	**123 (35,4)**	**130 (38,1)**
Mean diameter, cm	*Spruce*	15,4	14,0	**14.6**	17,7	15,6	**16,5**	25,3	23,7	**24.5**
	Birch	33,3	33,3	**33,3**	30,6	32,8	**31,6**	24,9	31,8	**27,7**

Trees of the biggest diameter classes represented the major share of mortality during the recent insect outbreak (Fig.6). Mean diameter of recently dead spruces at two transects was estimated as 24.5 cm (Table 1). Since initiation of insect outbreak the mean diameter of standing spruces dropped from 16.5 cm to 14.6 cm.

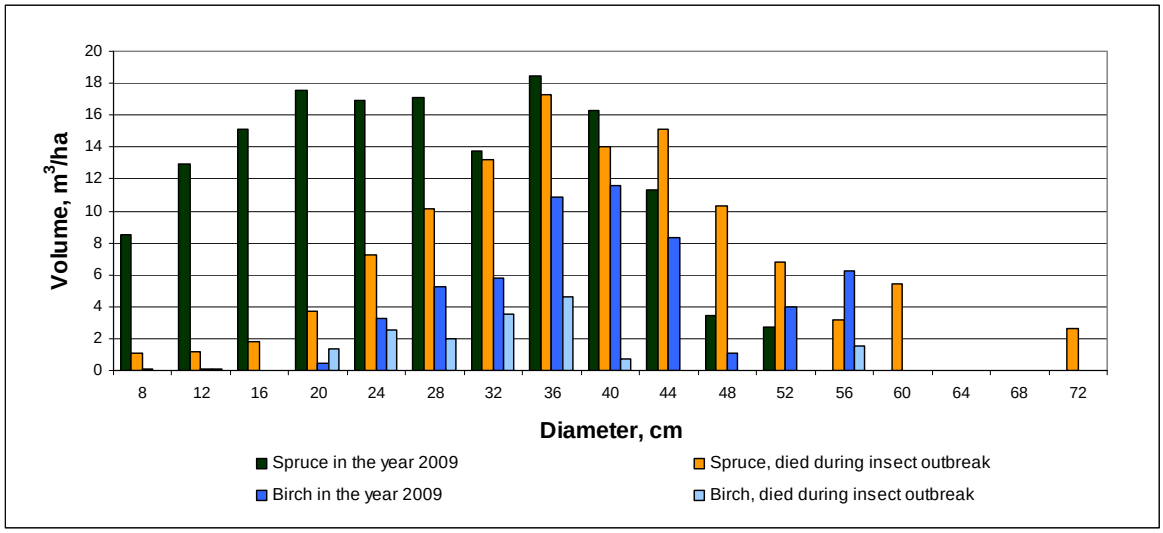


Figure 6. Distribution of standing volume and mortality (caused by recent insect outbreak, initiated in 2001), over diameter classes, depicted for two tree species – spruce and birch.

Spruce diameter distribution had not changed, and before and after insect outbreak revealed typical for old-growth forests inverse J-structure (Fig. 7).

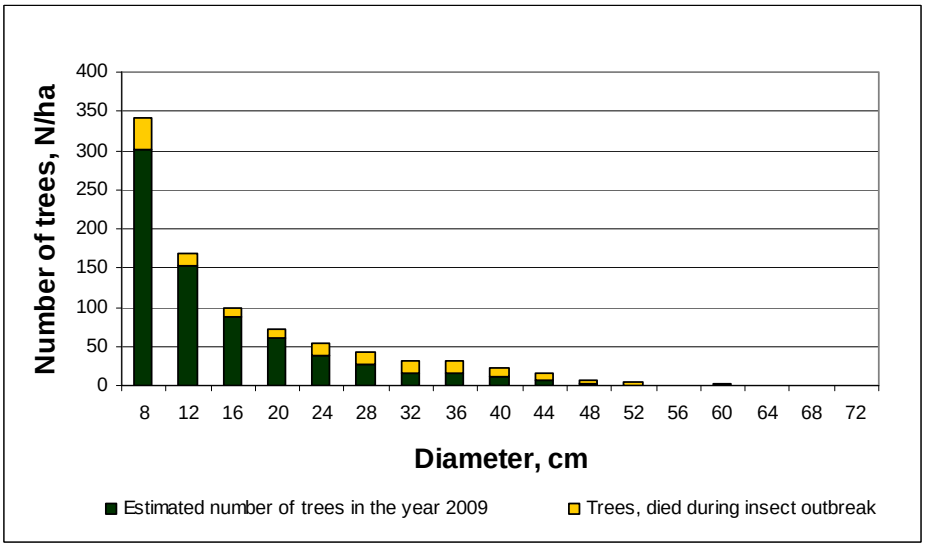


Figure 7. Diameter distribution, averaged for two transects and depicted for both: the year of insect outbreak initiation (2001) and the year of data collection (2009).

Soil moisture

Considerable difference in soil moisture was found among the sample plots and between the two transects. First transect had a higher soil moisture (Fig. 8).

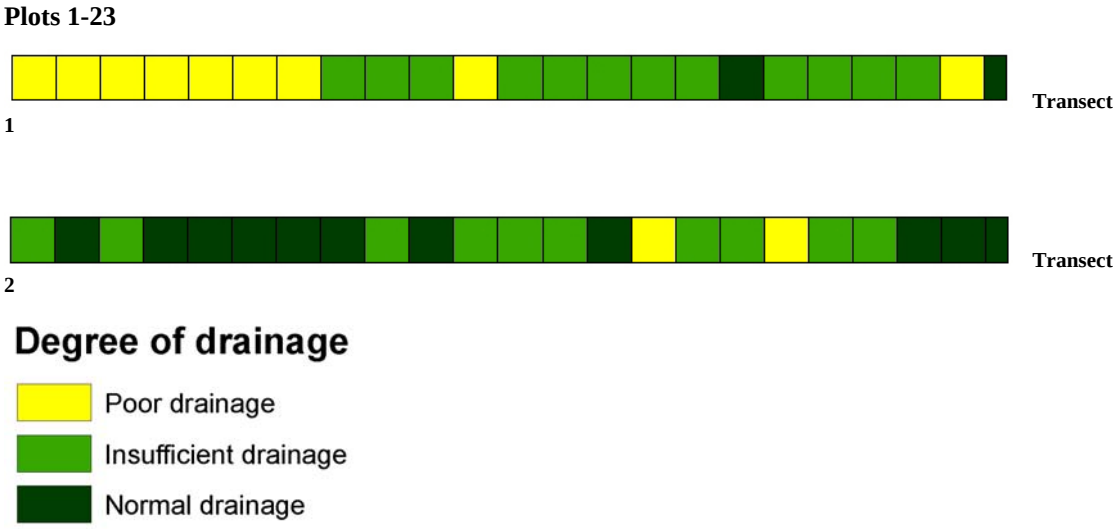


Figure 8. Variation of soil moisture characteristics (degree of drainage) along the two transects, defined for each sample plot by linking the percentage of sphagnum in the ground vegetation.

Age structure

Spruce age structure

Age structure of spruce depicted a multiple age distribution with pronounced regular peaks (cohorts). A minimum of four such peaks were distinguished (Fig.9). First cohort was peaking at the age of trees 260 years and enveloped the trees from 250 to 300 years old, second cohort – the trees of 200-250 years old, peaking at 210 years, third – was peaking at the age of 170 years and scattered between 150 and 200 years, and the youngest generations had their peak at the age of 110 years.

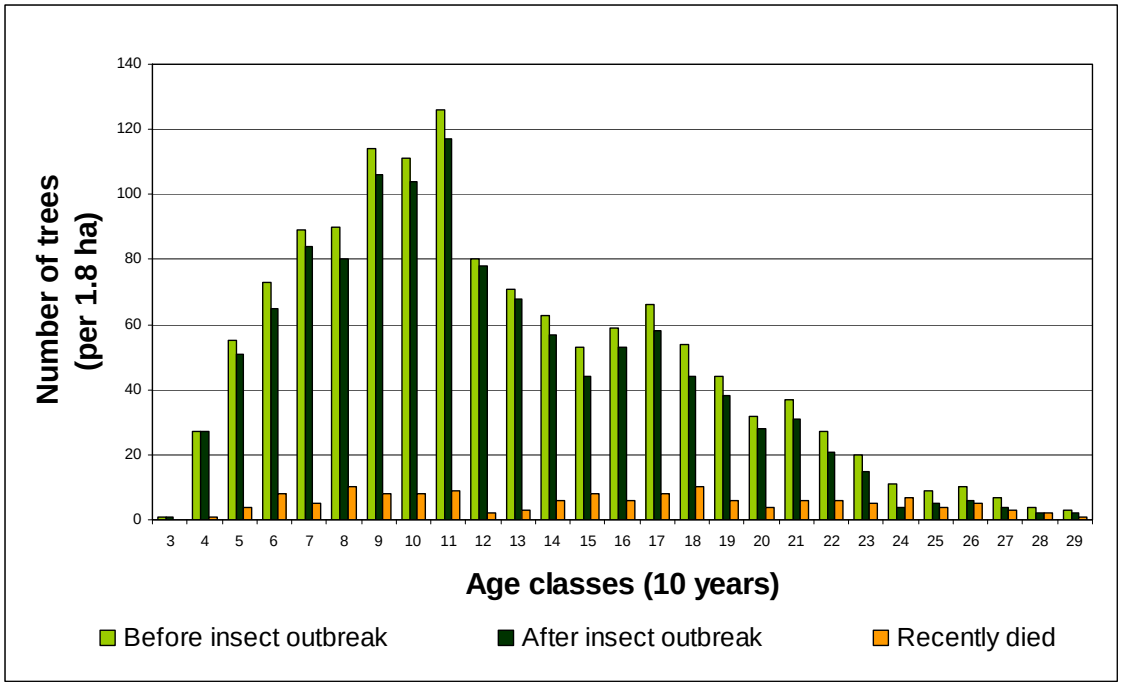
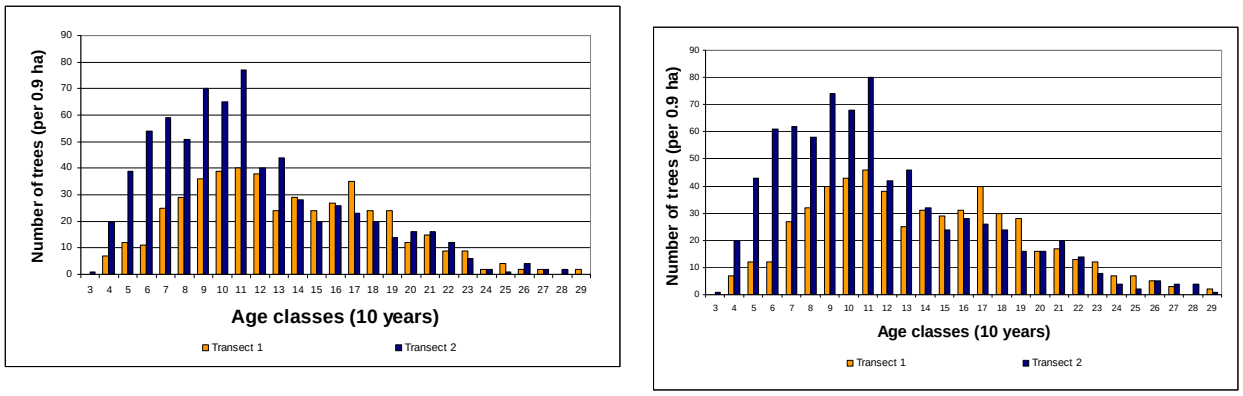


Figure 9. Age structure of spruce, presented as an absolute number of trees at 10-year age intervals, and considered for both transects. Data timed to the beginning and the end of the

most recent insect outbreak. Number of trees is calculated for the area of 1.8 ha. The age is determined at the height of 40 cm above the root collar.

Age structure of spruce did not significantly differ between transects and had synchronized pulses of regeneration in the past. Though we found more abundant regeneration of spruce on the second transect over the last century (Fig. 10).



a) b)

Figure 10. Age structure of spruce, defined for two transects separately. Number of trees was calculated for the area of 0.9 ha and presented at 10-year age intervals. The age was determined at the height of 40 cm above the root collar. Age structure is presented in relation to period of recent insect outbreak: is calculated for the year of data collection (2009) – figure (a), and reconstructed for the year of insect outbreak initiation (2001) – figure (b).

Recent insect outbreak did not strongly affect the age structure of spruce in the stands (Fig. 10).

Tree mortality, related to the last insect outbreak, was evenly distributed over the age classes (Fig. 9, 11) and did not significantly differ between the two transects (Fig. 11). Barely visible peaks in the age structure of recently dead spruces match with described spruce regeneration peaks (Fig. 9, 10, 11).

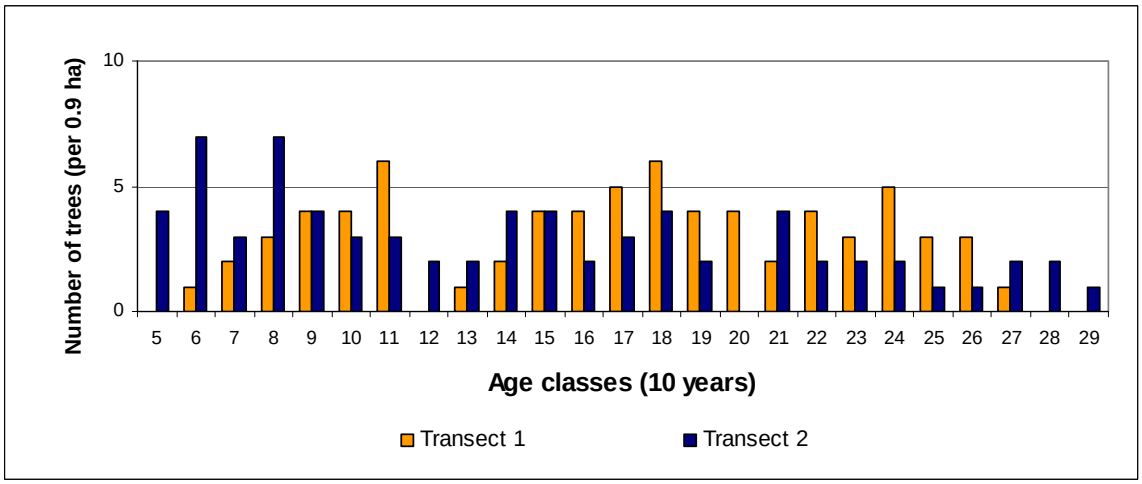


Figure 11. Age structure of spruce mortality, related to the recent insect outbreak (initiated in 2001), defined for each transect separately. Number of trees is calculated for the area of 0.9 ha. The age is determined at the height of 40 cm above the root collar.

Birch age structure

Birch was less abundant than spruce and its age structure was presented by clear separate cohorts (Fig. 12). Prevailing age of trees was from 141 to 210 years old. The regeneration of birch was more abundant at the first transect, the most significant difference between transects was found for birches of 120 and 180 years old.

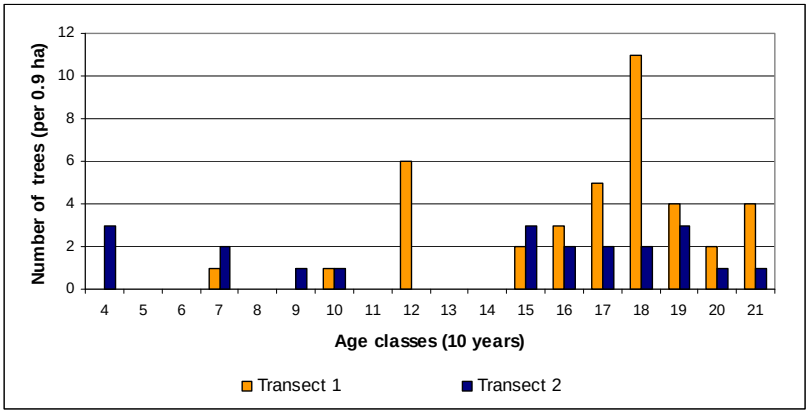


Figure 12. Age structure of birch, defined for each transect separately. Number of trees is calculated for the area of 0.9 ha. The age is determined at the height of 40 cm above the root collar. The total number of birch trees taken into account was 60 (out of 187 recorded in the stands).

Correlation of spruce ages with trees dimensions

We found a moderate correlation between DBH and age of spruces (R^2=0.47) (Fig. 13). Older trees however had the highest variation in diameters. DBH of trees older than 180 years differed from 6 to 54 cm (Fig. 13).

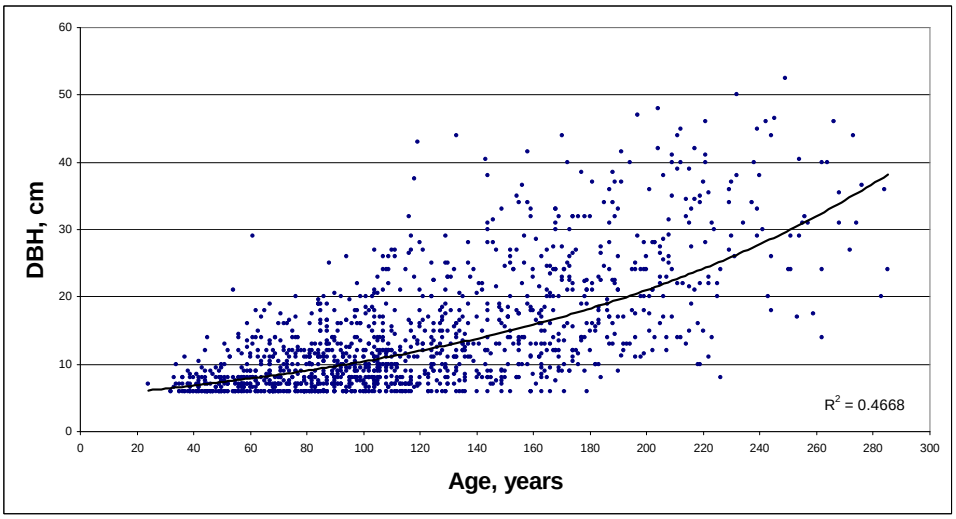


Figure 13. Correlation between DBH and age of spruces. Total number of trees included is 1336.

Mean age generally increased from understory to dominant canopy position classes, with large variability of ages observed within each class (Fig. 14). The largest variability was found for trees of intermediate canopy position. Their age varied from 31 to 290 years old.

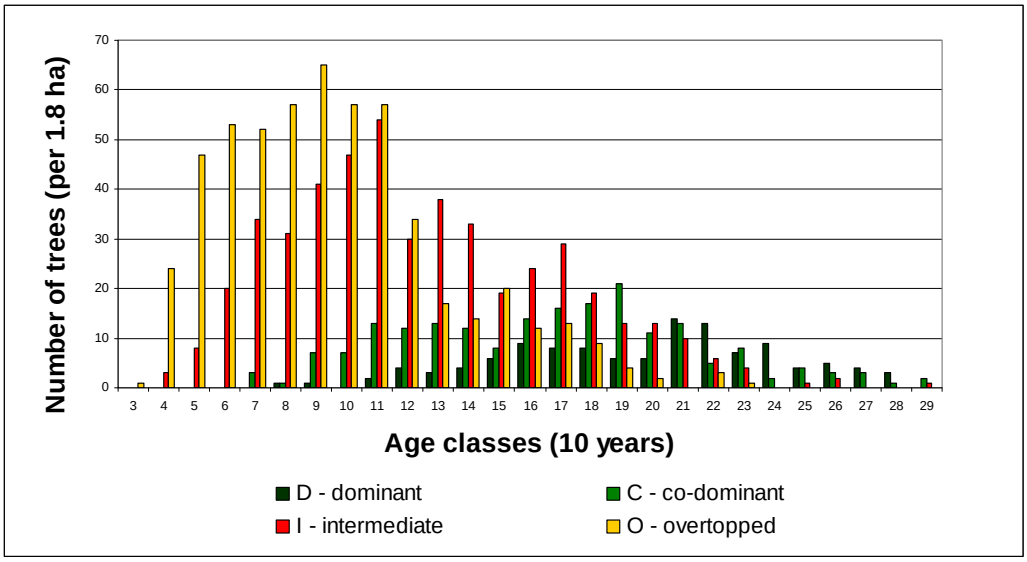


Figure 14. Age structure of spruces pertaining to different canopy positions (D - dominant, C – co-dominant, I - intermediate, O - overtopped). Number of trees is calculated for the area of 1.8 ha. The age is determined at the height of 40 cm above the root collar.

Disturbance rates

Percentage of released trees

Percent of released trees (considered as disturbance rate in many previous studies) significantly varied over the 280-year period (Fig. 15). Though low disturbance rates were more common for the whole studied time period: 40% of yearly rates revealed less than 1% of released trees, and 67% of rates were less than 2%. Mean yearly disturbance rate was 1.86 %. The peaks in disturbance rates commonly did not exceed 6% of released trees in the stands and were rather regular with the frequency of 30-40 years (Fig. 15).

The most recent peak in disturbance rate, calculated as release percentage, initiated after the year 2001 as trees reaction on severe European spruce bark beetle outbreak.

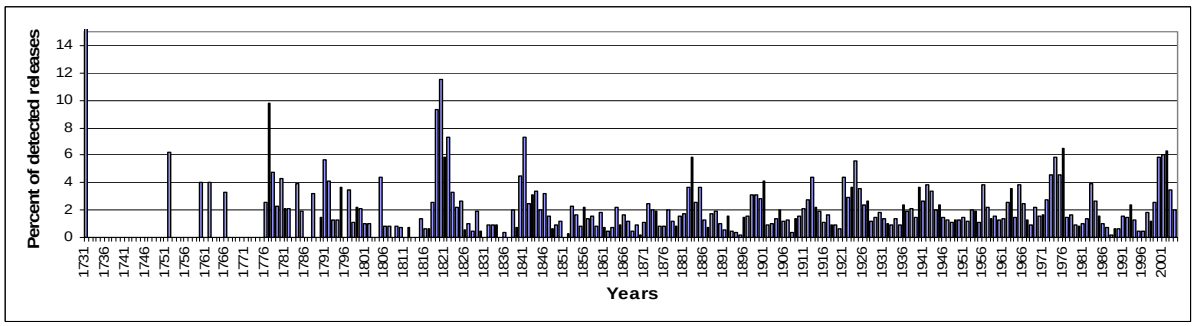


Figure 15. Yearly disturbance rates (percentage of released trees), averaged for both transects. Considered time span is from 1731 to 2004.

At decadal (10-year periods) scale release data revealed regular and clearly pronounced peaks in percentage of released trees (Fig. 16). Time between two neighboring peaks differed between 30 and 50 years. The decades with highest percent of detected releases were: 1980, 1930, 1890, 1850 and 1830-1820.

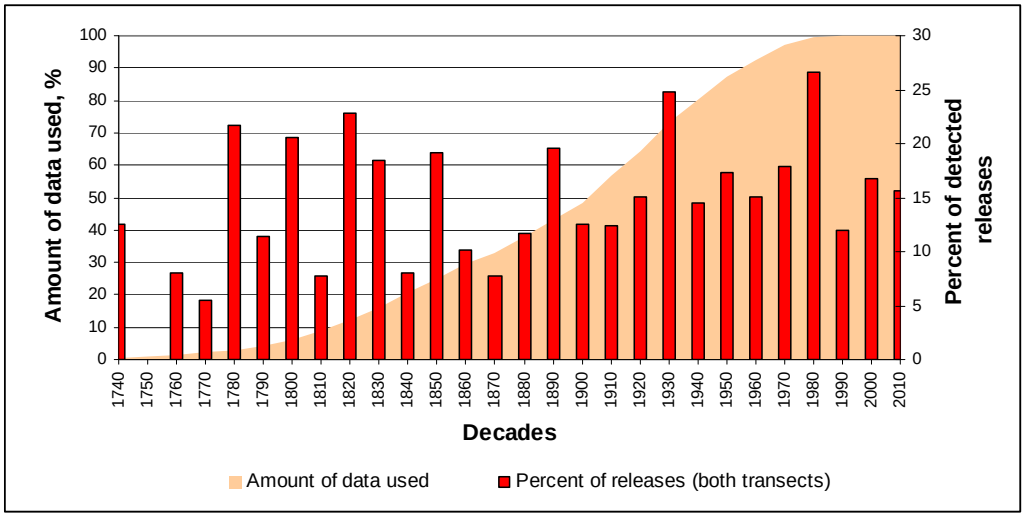


Figure 16. Decadal disturbance rates (percentage of released trees), averaged for both transects. Considered time span is from 1731 to 2004.

Pulses in disturbance rates were synchronous at both transects (Fig. 17). Higher rates, however were found at the 2th transect over the second half of the 20th century. On the contrary, higher density of releases was detected at the first transect over the earlier period before 1890 (Fig. 17).

This difference was more pronounced for decadal time sequence (Fig. 18).

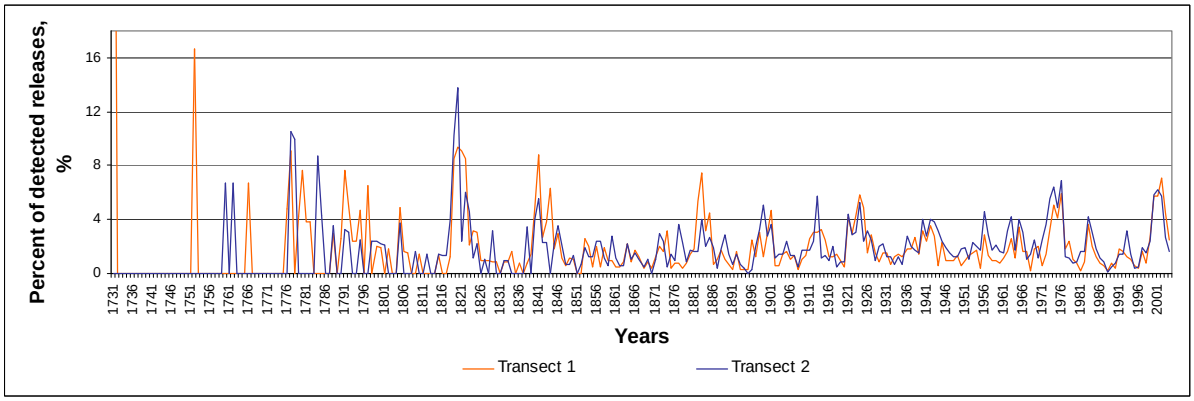


Figure 17. Yearly disturbance rates (percentage of released trees), considered for two transects separately. Considered time span is from 1731 to 2004.

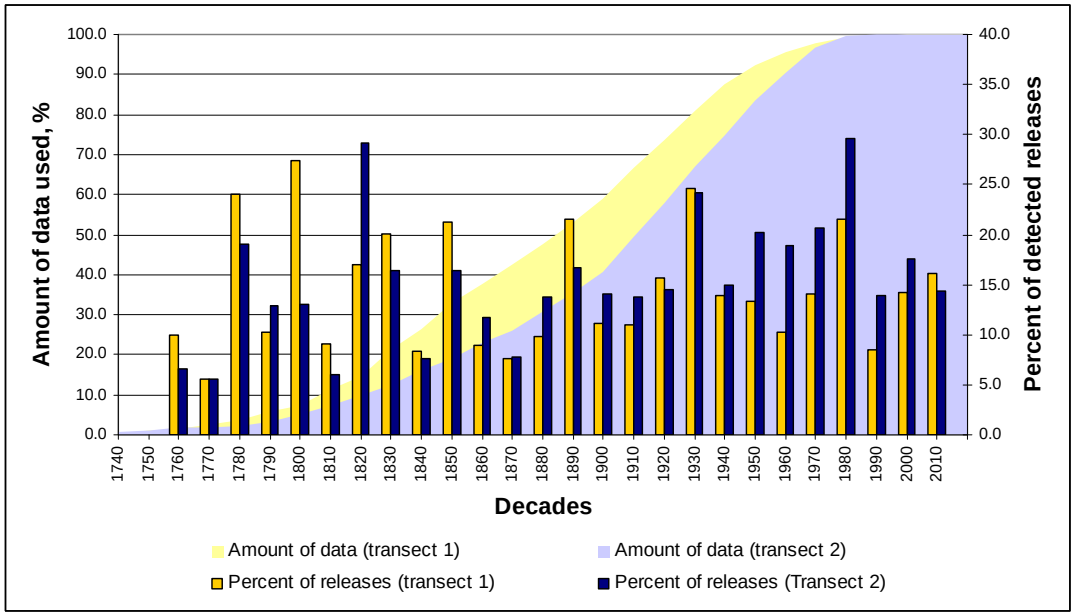


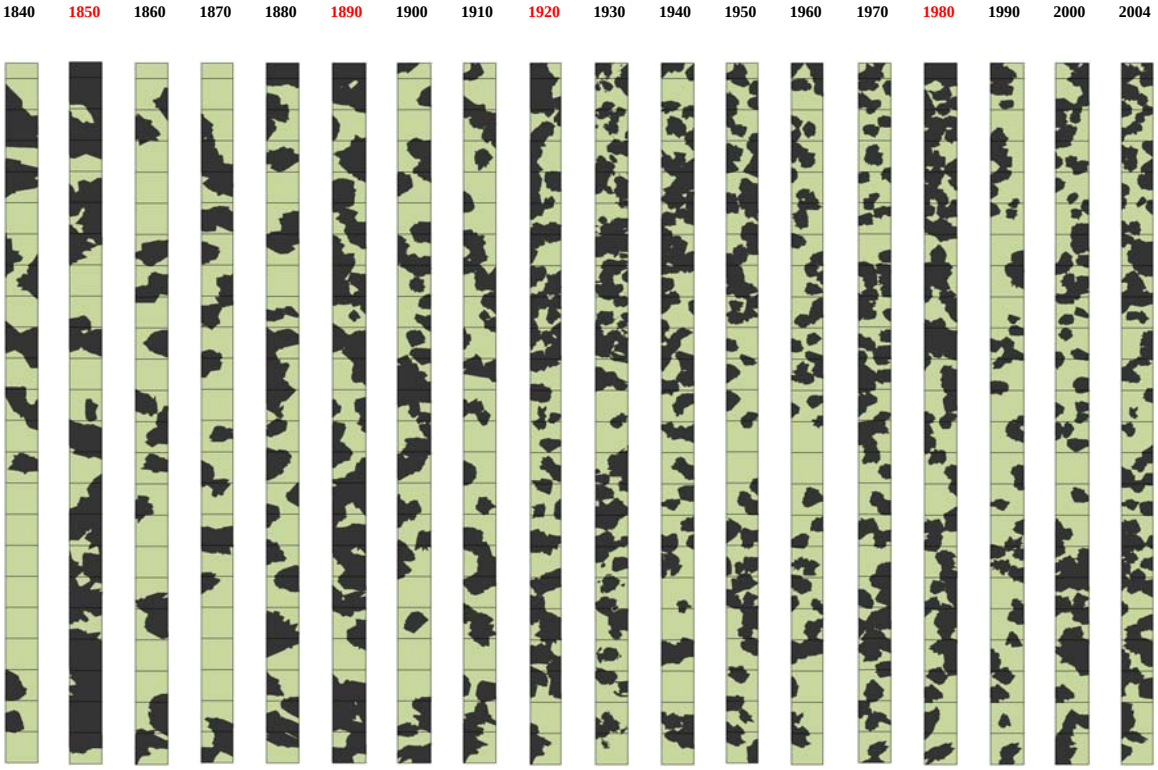
Figure 18. Decadal disturbance rates (percentage of released trees), considered for two transects separately. Considered time span is from 1731 to 2004.

Spatially reconstructed disturbance rates

Size of reconstructed canopy gaps differed from small (created by the death of one or several trees) to the middle-size gaps, occupied several sample plots (Fig. 19). The accuracy of reconstruction was diminishing towards the earliest decades (Fig. 19), due to less number of trees was used for gap delineation.

Table 2

Transect 1



Transect 2

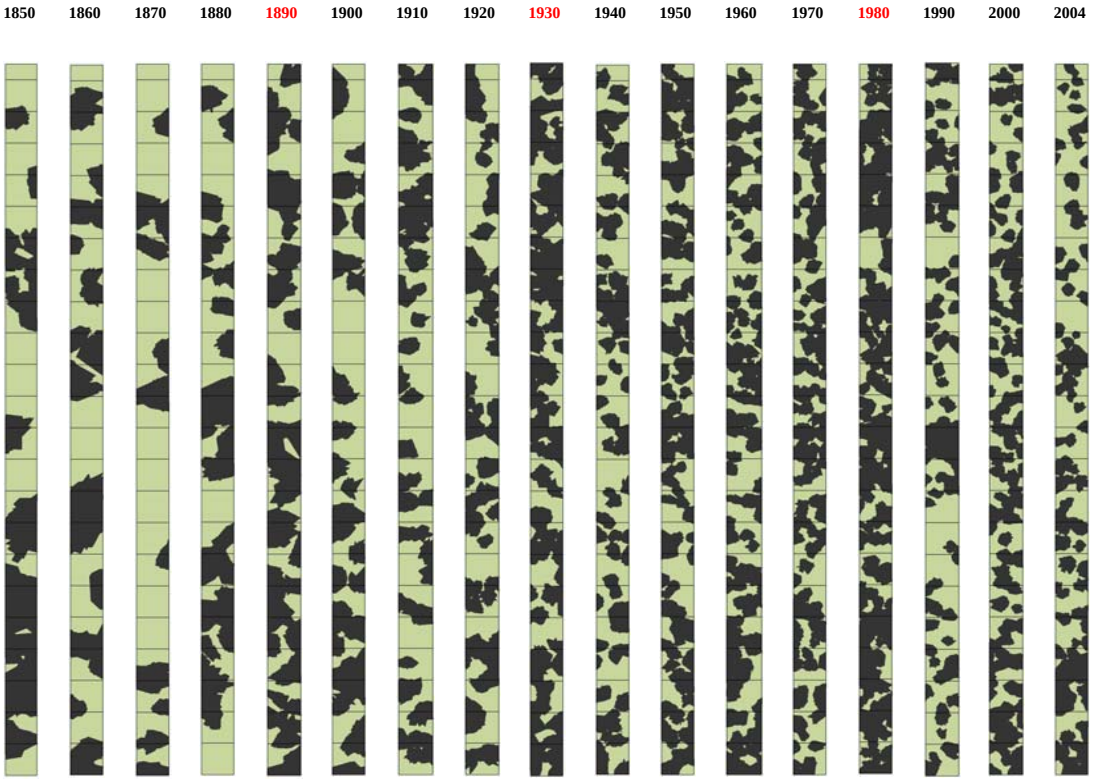
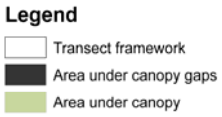


Figure 19. Spatially explicit decadal disturbance rates, reconstructed in ArcMap 9.3 for the time span 1831(1841) – 2004.



About 40% of disturbed area per decade was constantly present in the forest canopy over the last 170 (160) years (Fig. 20).

Pulses of disturbances, found in percentage of released trees, have been mirrored in reconstructed disturbance rates, based on spatial data. Regular peaks in disturbance rates never exceeded 75% per decade and normally were about 60% of area disturbed (Fig. 20). Disturbance pulses were synchronized between transects. Second transect revealed more pronounced peaks of disturbance rates over the 20th century comparing to the first transect (Fig. 20).

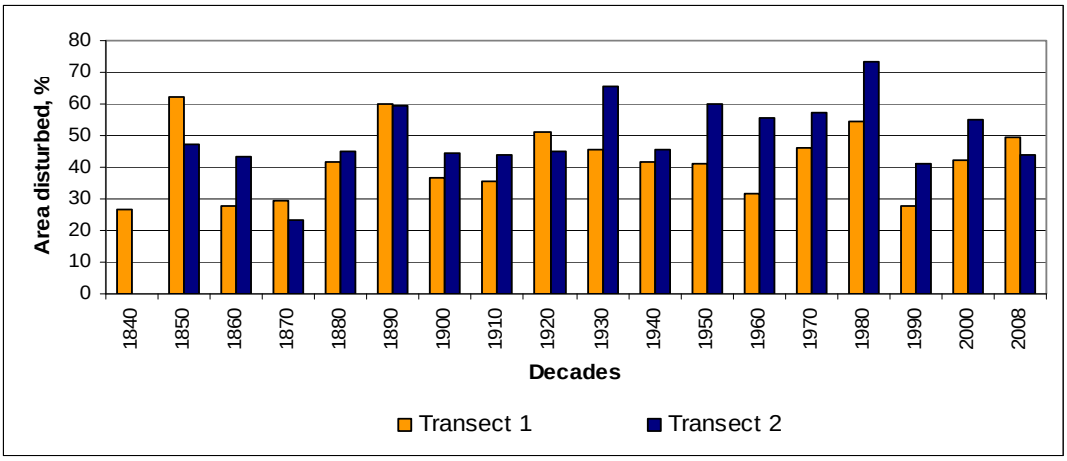


Figure 20. Spatially explicit decadal disturbance rates, considered separately for two transects. Considered time span is from 1731 to 2004.

Influence of soil moisture on disturbance regime.

No significant difference was observed in disturbance rate fluctuation in the forest with different soil moisture. Only slightly higher disturbance intensity and more pronounced peaks in disturbance rates were found in the stands with higher soil moisture (normal and insufficient degree of drainage) (Fig. 21).

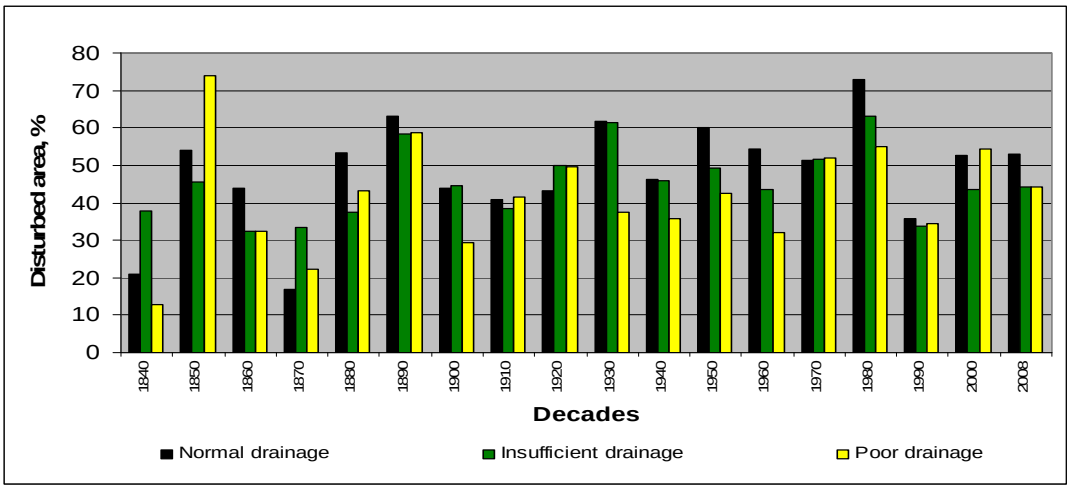


Figure 21. Spatially explicit decadal disturbance rates, calculated for stands with different soil moisture (degree of drainage), given as proportion of disturbed area within plots with similar drainage conditions. Considered time span is from 1731 to 2004.

Discussion

Age structure

We found the age structure of spruce to be of all ages. This corresponds to the typical characteristics of late-successional boreal forest, lacking stand replacing disturbances over a long period of time (Shorohova et al., 2009). We identified four regular peaks in the spruce age structure, indicative of four regeneration episodes, occurred with the frequency of 40-60 years (Fig. 9, 10). These episodes were strongly synchronized at the two transects, however the abundance of spruce regeneration was different. The number of young trees, originated over the last century at the second transect was nearly twice this number at the first transect. This is likely connected the deficit in soil moisture found on the second transect. Moisture deficit, is an important growth-depressing factor in this area, which in connection to periodical summer droughts might have caused periodical increases in disturbance rates (Aakala and Kuuluvainen, 2010), underlying episodic forest regeneration.

Usual light regime under the forest canopy largely limited birch regeneration. Share of birch apparently was increasing following increases in disturbance rates. In the earliest decades of considered time period (about 141 - 210 years ago) birch regeneration was more abundant (Fig. 12), which may indicate extensive openings in the forest canopy about that time.

Temporal patterns of spruce and birch regeneration have shown considerable degree of synchronicity. Some spruce cohorts (trees of 110 and 170 years old) were obviously timed to the same origination events as birch (trees of 120 and 180 years old). The difference in 10 years can be explained by ability of birch seedlings to reach the height of core extraction much faster than spruce.

General discussion of forest disturbance history

We found no evidence of stand replacing disturbances in the studied forest at least over the last 300 years. The age distribution of oldest trees did not suggest a major distrurbance event at the start of the study period since all of them were characterized

by slow initial radial growth (less than 1.5 cm per year). This lets us claim that early parts of the spruce growth occurred under closed canopies. Thus the main forest canopy remained continuously in the studied forests over more than 300 years.

Reconstructed disturbance history suggests that small and middle scale canopy disturbances prevailed in the stands, as it was described for forests, dominated by shade-tolerant dark coniferous species (spruce, fir) at the flat watersheds European boreal zone (Yaroshenko et al., 2001; Dyrenkov, 1984). It is unlikely that forest fires occurred in the area during the studied period. We found no charcoal and no pines in the sampled area and its vicinity.

Periodic deviations from low disturbance rates likely played a major role in forest regeneration and tree species dynamics. We identified four regular large disturbance episodes over the period of time from 1831 to 2004 (the number does not include the most recent insect outbreak), occurred at the average frequency of about 40 years. Reconstructed large disturbance episode in decade 1890 coincides with historically recorded massive insect outbreak, initiated at the end of 19th century (Kuznetsov, 1912).

Disturbance dynamics did not significantly differ between two transects. It is clear for the whole reconstructed historical period. First possible implication is that reconstructed disturbance history is characteristic for all the major considered forest types of the studied area (i.e. central part of the large flat watershed in taiga zone, dominated by spruce stands). Another implication suggests high probability of climate signal in reported release chronology. However this question needs additional detail consideration.

Disturbance rates

We described disturbance rates at the temporal and spatial scale. The annual disturbance rate was estimated to be 4% and the rate at peaking decades was about 60%. These values were calculated by GIS-aided analysis using information on trees allocation and their growth response to local canopy destruction over time. There are no studies yet to make a comparison of these results with. We assume however the calculated percent to be rather high for sustained stand development over at least three centuries. The possible explanation of overestimation is that the resulted disturbance rates likely include interspaces between canopy trees, or/and some canopy gaps at neighboring decades might overlap, due to settled disturbance reconstruction method.

Commonly disturbance rate calculated as percentage of detected releases. Our estimate of mean yearly disturbance rate equals 1.8% of released trees. About 67% of disturbance rates were lower than 2%.

In the previous studies we find much lower estimations. Most of them were conducted in the small old-growth forest patches, maintained within the highly fragmented forest landscapes, or in the mountain areas.

In the mountain *Picea rubens* dominating forests in Northern America the overall mean disturbance rate was estimated in 10.1% per decade (Fraver and White, 2005a) and later in 9.6% per decade (Fraver et al., 2009), which is nearly twice lower, than in given study. Fraver also admits the absence of stand replacing disturbances over 120 – 180 years of studied forest history.

In later study in the Northern American forest, composed by *Picea rubens* and *Abies balsamea,* Rowland and White estimated mean decadal disturbance rate as 5 – 10% over considered 150 – 300 years (Rowland and White, 2010).

In the mixed forest with *Acer saccharinum* and *Tsuga canadensis* average mortality rates were 5.7 – 6.9% per decade (Frelich and Lorimer, 1991). Authors note specific clustering of heavy disturbances. However these results would be hardly comparable with results of our study due to significant differences in forest types. More comparable estimations of annual mortality were earlier reported by Hyttebon – 1.12% (Hytteborn et al., 1991). The annual mortality, found in Scandinavian coniferous forests, was much lower. In the *Picea abies* dominated forests in boreal Sweden the annual mortality rate was 0.6% (Fraver et al., 2008). Earlier in mixed-species forest in Swedish boreal zone Linder found annual mortality rate 0.45% (Linder, 1998). Aakala made his short term studies, based on dating the year of trees death, in old-growth spruce forests in Finland and Murmansk province of Russia, and found 0.3% annual mortality over the last 35 years (Aakala et al., 2009).

Influence of soil moisture on disturbance regime.

We found little effect of soil moisture on disturbance history. The fluctuations of disturbance rates were synchronized between forests of three different soil moisture regimes (Fig. 21). This indicates that climatic anomalies might have been an important prior factor of the major disturbance episodes.

Earlier, the absence of any significant difference in disturbance regimes between different forest stands was reported in Northern America in the stands, composed by *Acer saccharinum* and *Tsuga canadensis* (Frelich and Lorimer, 1991) and in the mountain old-growth forest landscape in the Big Reed Forest Reserve, Northern Maine, USA (Fraver et al., 2009).

Forest stands with higher soil moisture were characterized by a slightly lower disturbance rates with smoother peaks (Fig. 21). Moisture deficit, apparently, in combination with some exogenous factors, increases disturbance intensity. Study of this question in the southern parts of the same watershed area, referred to the most recent large disturbance event, revealed the summer droughts in condition of moisture deficit to be the major growth-depressing factor (Aakala and Kuuluvainen, 2010).

Advantages and disadvantages of the methods used

The current approach to detect radial growth releases reveals certain advantages and disadvantages to reconstruct disturbance history. The main advantage of setting the strict criteria for release detection is minimization of subjective decisions which could have been done while using other methods. Another advantage is the use of spatial information to verify results of release detection algorithm.

There are, however, several disadvantages of the used release detection method. By its definition *release* is an increase in radial growth which must be *abrupt*, *sustained* and *sizable*. In terms of this definition, we came across several unsolved problems:

1) Compression wood, often present at the earliest parts of growth chronologies, was not possible to sort out by running averaging. Thus compression wood signals might be included into the study results.

2) At some periods spruce radial growth was extremely slow, because of this reason even insignificant absolute increase might have been considered as 100% abrupt increase of mean ring width. Such pseudo-releases were also not excluded from the disturbance rate.

Future research directions

Currently, we used only the formal approach for release identification. In the future research we would like to modify this approach and make a final decision about release presence by setting the absolute increase threshold and by looking at each chronology individually (Fraver and White, 2005b).

There is a potent in using data fromgap-recruited birch trees as supplementary evidence of canopy disturbances. Abundant birch regeneration at certain periods might indicate pulses of disturbance rate and increase of the mean gaps size (Drobyshev, 1999).

Furthermore, several additional studies can be made based on same data source.

1) Finding trends and correlations between reconstructed disturbance rates and climate data.

2) Estimating the role of different factors (e.g. insect outbreak, wind-through and others) by estimating prevalent gaps size.

As a final step, we would like to formulate some forest management recommendations for reconstruction of degraded forest ecosystems and measures to improve existing management approaches towards more nature friendly.

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